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CRETACEOUS ANGIOSPERM POLLEN OF THE ATLANTIC COASTAL PLAIN AND ITS EVOLUTIONARY SIGNIFICANCE

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ONE OF THE MAJOR problems in the study of the evolution of higher plants is the paucity of evidence from the fossil record on the origin and evolution of the angiosperms. Because of the relatively sudden appearance of angiosperms in the fossil record, the lack of recognized angiosperm precursors, and the lack of any striking peculiarities of the macroscopic remains of Lower Cretaceous angiosperms (mostly leaves), almost all conclusions on the origin of the group and the nature of its primitive members have been based on comparative studies of its living representatives. Angiosperm paleobotany has been primarily concerned with the geographic vegetational and floristic changes in the Tertiary, which were due more to migration and extinction than to evolution. The methods of Tertiary angiosperm paleobotany, such as the procedure of identifying modern taxa for paleoecological information, have been far less productive in the Cretaceous, and the problematical nature of the results is undoubtedly largely responsible for the present low level of activity in Cretaceous megafossil paleobotany.

In the past decade a new method has been applied in Cretaceous paleobotany which promises to shed light on the problems of angiosperm origin and evolution. This is the study of fossil pollen and spores. In contrast to the megafossil record, the palynological record shows clear-cut changes in the morphology and diversity of the angiosperms from the time of their first appearance. Most of the information on early angiosperm pollen has been obtained for stratigraphic purposes (cf. Couper, 1964), and is, from a botanical point of view, largely descriptive; the evolutionary implications have been frequently mentioned but not discussed in detail.

The purpose of this paper is to review the characteristics of Lower and early Upper Cretaceous angiosperm pollen floras and to discuss the evolutionary and phylogenetic implications of the record. Much of this discussion is based on my own work on Cretaceous angiosperm pollen of the Atlantic Coastal Plain, which appears to give a fairly representative picture of the world flora. Comparisons will be made with correlative sequences, which are now known in many other parts of the world. Much of the detailed documentation of both the stratigraphic and systematic aspects is in progress and will be presented later in more complete form, but the general results seem clear enough to be summarized in this preliminary paper.

In general, morphological terminology follows Erdtman (1952), though some terms of Pflug (1953) are used in discussing triporate pollen.

GEOLOGICAL BACKGROUND

The Cretaceous is one of the longer geologic periods, covering some 72 million years between about 136 and 64 million years before the present (Casey, 1964). The Cretaceous System is customarily divided into Lower and Upper Cretaceous series, which are subdivided into six stages each (TABLE 1). These stages were first recognized in western Europe and subsequently extended around the world; they are now operationally defined by ammonite zones of the Tethyan province.

Continental or near-shore marine sediments favorable for palynological studies are fairly extensively developed in the Cretaceous, though few areas have large parts of the system represented by continuous continental deposition. For example, the uppermost Jurassic and much of the Lower Cretaceous are well represented in the Purbeck and Wealden of southern England, but late Lower Cretaceous rocks there are marine and only marginally suitable for palynological study. The Upper Cretaceous consists of the wholly unsuitable marine Chalk, and to extend the European Cretaceous pollen record we must go to Central Europe.

TABLE 1. **Subdivisions of the Cretaceous**

SERIES	STAGES	
UPPER CRETACEOUS	Maestrichtian	
	Campanian	Senonian (most common usage)
	Santonian	
	Coniacian	
	Turonian	
	Cenomanian	
LOWER CRETACEOUS	Albian	
	Aptian	
	Barremian	Neocomian (most common usage)
	Hauterivian	
	Valanginian	
	Berriasian	

TABLE 2. **Presumed stratigraphic relations of Atlantic Coastal Plain nonmarine Cretaceous formations**

TIME-STRATIGRAPHIC UNITS		ROCK-STRATIGRAPHIC UNITS				
SERIES	STAGES	SOUTHERN AND CENTRAL MARYLAND AREA			RARITAN BAY AREA, NEW JERSEY	
	—?—?—?—					
	Santonian	Magothy Formation			Magothy Formation	Cliffwood Beds Morgan Beds Amboy Stoneware Clay
	—?—?—?—	Hiatus			Hiatus	
	Coniacian					
	—?—?—?—					
Upper	Turonian				Raritan Formation	Old Bridge Sand South Amboy Fire Clay Sayreville Sand Woodbridge Clay Farrington Sand Raritan Fire Clay
	—?—?—?—					
	Cenomanian				Subsurface Only	
			"Raritan" Formation			
—?—	—?—?—?—	Potomac Group	Patapsco Fm.	Subzone B —Zone II— Subzone A		
	Albian					
Lower	—?—?—?— Aptian Barremian?		Arundel Clay Patuxent Fm.	Zone I		

An excellent section of the late Lower and early Upper Cretaceous for pollen studies is found in the Atlantic Coastal Plain between Virginia and New Jersey. Pre-Campanian deposition in this area took place mostly in river flood plains and deltas. The result is a seaward-dipping wedge of unconsolidated clays, sands, and gravels, often very rich in organic matter, which is exposed as a wide northeast-trending band several hundred feet thick at the landward margin of the Coastal Plain. The presumed stratigraphic relations are shown in TABLE 2.

In Maryland and adjacent states the basal unit is the Potomac Group, which until recently was defined as consisting of the Lower Cretaceous Patuxent, Arundel, and Patapsco formations (cf. Clark *et al.*, 1911). The Patuxent tends to be feldspar-rich and sandy or gravelly; the Arundel is a huge lens of dark, organic-rich clay with siderite nodules, while the Patapsco is rather heterogeneous, though its red and variegated clays are most characteristic. As is often the case with continental sediments, Potomac Group lithologies are highly variable, and there is much doubt that the formations can be consistently separated in the field. The Arundel, which was apparently deposited in a swamp belt, is the greatest exception to this, and it is an important marker in dividing the Potomac Group; however, it is definitely present only in the area between Washington, D.C., and Baltimore Co., Maryland.

To these three formations have recently been added higher beds traditionally designated Raritan Formation (Weaver *et al.*, 1968), which appear to be earliest Upper Cretaceous. These sediments are generally sandy and lacking in fossils; the few samples that have been examined palynologically (discussed below) indicate an age between the typical Patapsco and the type New Jersey Raritan. In the absence of any distinctive lithological similarity to the type Raritan, this Maryland "Raritan" should probably be considered either part of the Patapsco or a new formation of the Potomac Group.

In the Raritan Bay area of New Jersey, Coastal Plain deposits begin with the Upper Cretaceous Raritan Formation, which appears to be largely of deltaic origin (Owens *et al.*, 1968). The Raritan has been divided into six locally recognizable members, excluding the Amboy Stoneware Clay, which on palynological and other grounds is better associated with the overlying Magothy Formation (Wolfe & Pakiser, ms.). The palynologically important Woodbridge Clay member is dark, massive, highly organic, and siderite-bearing, like the much older Arundel Clay of Maryland, but the South Amboy Fire Clay member is more varied lithologically, with lignitic beds and sands as well as dark, often laminated clays. Most of the Raritan Formation consists of deltaic sands.

The last nonmarine Cretaceous unit, the Magothy Formation, occurs in both Maryland and New Jersey. It unconformably overlies both the Potomac Group and the Raritan Formation; this unconformity represents a considerable hiatus in deposition even in New Jersey, where older Upper Cretaceous is present. The Magothy is lithologically distinctive and unlike the lower units: it consists mostly of alternating sands and dark clays with considerable lignitic material, and it shows much more continuity of individual beds. It appears to be a deltaic deposit, with evidence of tidal influence (Glaser, 1967); it is overlain by the often glauconitic offshore shelf sediments of the Matawan and Monmouth groups.

Unfortunately, controls on the age of the Atlantic Coastal Plain continental units from marine fossils are poor. Except for an aberrant brackish water fauna of uncertain age from a deep well on the Eastern Shore of Maryland (Anderson, 1948), marine fossils are unknown in the Potomac Group. Marine mollusks from the Woodbridge Clay in New Jersey, recently restudied by Sohl (pers. comm.), date that unit as middle or late Cenomanian, while a late Santonian ammonite was recently found in the Magothy Formation of New Jersey (Owens & Sohl, pers. comm.). Biostratigraphic correlations must therefore be based almost entirely on the plant fossils, of which the pollen and spores are by far the most useful and readily obtained. Palynological study reveals a sequence of biostratigraphic zones which are consistent with the regional lithostratigraphy, and which compare closely with better dated sequences in other parts of the world. It is the angiosperms, which were apparently undergoing rapid evolutionary diversification in the mid-Cretaceous, that are most useful in defining these zones. Though questions might be raised on the exact correlation of the angiosperm pollen assemblages in the absence of independent age control, the relative times of appearance of major types are the same as elsewhere, and correlations based on the angiosperms agree well with those made with the spores and gymnosperm pollen alone.

PATUXENT AND ARUNDEL FORMATIONS

The pollen and spore flora of the lower two formations of the Potomac Group, first described in detail by Brenner (1963), is representative of mid-Lower Cretaceous floras of most of the world, just before the appearance of typical angiosperm pollen. It is dominated by pteridophytes and gymnosperms, notably: the fern families Cyatheaceae (or Dicksoniaceae), Schizaeaceae (*Cicatricosisporites*, *Appendicisporites*, and possibly *Trilobosporites*, *Concavissimisporites*, etc.), and Gleicheniaceae, as well as groups of less certain affinities; conifers representing the living families Pinaceae, Podocarpaceae, Cupressaceae (or Taxodiaceae), and Araucariaceae, and extinct forms such as *Classopollis* (which was apparently produced by plants known as the megafossil genera *Cheirolepidium*, *Brachyphyllum*, and *Pagiophyllum*, Pocock & Jansonius, 1961), the possibly related *Exesipollenites tumulus* Balme, and the last of the seed ferns, the Caytoniales (*Vitreisporites*). Smooth monosulcate grains probably represent the gymnospermous orders Cycadales, Bennettitales, and Ginkgoales, while the Gnetales are represented by grains of the *Ephedra* type. The picture of the flora obtained from the pollen and spores is in general agreement with that provided by the megafossils, which are also predominantly ferns, conifers, and cycadophytes (Fontaine, 1889; Berry, 1911).

The genus *Eucommiidites*, common throughout the Potomac Group, is of special interest since it was first described by Erdtman (1948) as a dicot from Jurassic rocks. *Eucommiidites* pollen is smooth and medium-sized, with three furrows which initially suggest the tricolpate condition typical of and restricted to dicots (FIGS. 1a,b). However, one of the furrows is wider and more cycad-like than the others, and the general shape of the grains was shown by Couper (1958) to be more like that of monosulcate gymnosperm than tricolpate angiosperm grains. Subsequently, *Eucommiidites* has been found in the micropyles of gymnospermous seeds in both England (Hughes, 1961a) and Virginia (Brenner, 1963). It was presumably produced by an extinct group of gymnosperms.

The Patuxent-Arundel flora does include one form, *Clavatipollenites* Couper, which has distinctive angiosperm characters. *Clavatipollenites* is generally monosulcate, with the exine finely pilate (clavate), retipilate (with free pila arranged in a reticulum), or reticulate (with the heads of the pila fused to form a true reticulum). Couper (1958), in describing the type species *C. hughesii* from the Barremian of England, pointed out that while the monosulcate aperture condition is prevalent in gymnosperms, pilate or retipilate sculpture is not known outside the angiosperms, and he noted the similarity of the grains to those of *Ascarina* in the dicot family Chloranthaceae. *Clavatipollenites* has been widely reported from the middle and late Lower Cretaceous: the Barremian through Albian of England (Hughes, 1958; Kemp, 1968), the Aptian and Albian of Portugal (as *Apiculatisporis vulgaris* Groot & Groot, 1962), the Barremian through Albian of West Africa and the Aptian and Albian of Central America (Couper, 1964), the Albian of Australia (Kemp, 1966), presumed pre-Albian rocks of southern Argentina (Archangelsky & Gamerro, 1967), and the late (Norris, 1967) and middle (pers. obs.) Albian of the Canadian Plains. A supposed latest Jurassic or earliest Cretaceous species, *C. couperi* Pocock, from Canada (Pocock, 1962) and Egypt (Helal, 1966) is dissimilar in its exine structure and is probably a cycadophyte (Pocock, pers. comm.; cf. Kemp, 1968).

Clavatipollenites is so variable that it undoubtedly represents several natural species. The coarseness of the sculpture varies greatly, and there is every degree of fusion of the heads of the pila, up to a good reticulum with large lumina. The grains usually have a simple sulcus, consisting of a granulate or irregularly sculptured area in the pilate forms (FIGS. 1c–e), or a well-delimited unsculptured membrane in the reticulate ones (FIGS. 1f,g). But especially in the overlying Patapsco Formation, the pilate grains often have a more irregular, sometimes trichotomosulcate aperture (FIG. 1h), as figured by Groot and Groot (1962) as *Apiculatisporis vulgaris* from Portugal, or they may be inaperturate or have several weak colpoid areas (FIG. 1i).[1]

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[1] Recently Hedlund and Norris (1968. Spores and pollen grains from Fredericksburgian (Albian) strata, Marshall County, Oklahoma. Pollen et Spores **10**(1): 129–159) have described polycolpoidate and tetra- and pentachotomosulcate grains from the Middle Albian as species of *Stephanocolpites* and the new genus *Asteropollis*. These grains appear to be essentially identical to the irregular-aperturate specimens of *Clavatipollenites* from the Potomac Group, but they show much more complete

The distinction between retipilate grains with an irregular sulcus and reticulate grains with a clearly defined sulcus and a tendency for the reticulum to detach is important in Kemp's (1968) separation of *Clavati-*

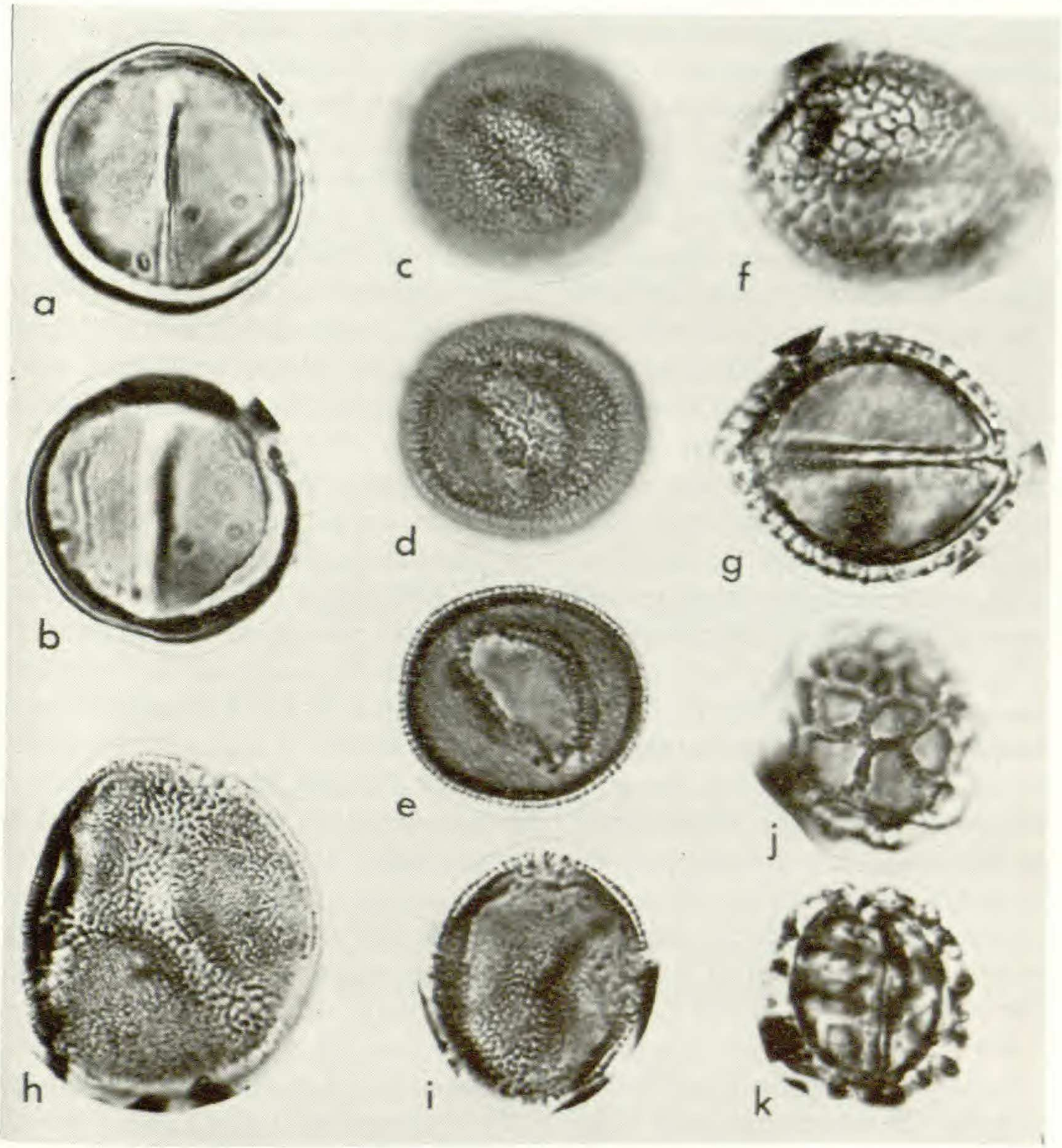

FIG. 1. Potomac Group gymnosperm and probable angiosperm pollen. Numbers in parentheses refer to slides. a and b, *Eucommiidites troedssonii*, grain with main sulcus on upper side, two focal levels (Aq 45–1c: Patuxent Fm., Zone I); c, d, and e, *Clavatipollenites* sp., flattened pilate grain with sulcus on lower side (Aq 27–1g: Patuxent Fm., Zone I); f and g, *Clavatipollenites* or *Liliacidites* sp., reticulate grain, two focal levels (Aq 44–1a: Patuxent Fm., Zone I); h, *Clavatipollenites* sp., trichotomosulcate grain (B 27–1c: Patapsco Fm., Subzone B of Zone II); i, *Clavatipollenites* sp., tetracolpoidate grain (65–1–2a: Patapsco Fm., Subzone B of Zone II); j and k, *Peromonolites* sp. (*sensu* Brenner), grain with sulcus (?) on lower side, two focal levels (Aq 18–1c: Patuxent Fm., Zone I). All figures × 1000.

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intergradation from sulcoidate to colpoidate. This gives further support to the hypothesis that zonaperturate (including tricolpate) pollen is derived from monosulcate through tri-, tetra-, or pentachotomosulcate intermediates.

pollenites hughesii and her species *C. rotundus*. She also found size and shape were reliable characters, but the retipilate forms in the Potomac Group are much more variable in size and shape than *C. hughesii* in England, overlapping considerably with *C. rotundus*, while the reticulate forms often lack the characteristic infolding of the sulcus margin of *C. rotundus* and sometimes have coarser sculpture. Brenner (1963) referred the reticulate forms, which he reported only from the Patapsco, to *Liliacidites dividuus* (Pierce) Brenner. However, the *Liliacidites* type intergrades with *Clavatipollenites* and does occur occasionally in the Patuxent-Arundel, favoring Kemp's treatment of both types as one genus. The status of *C. minutus* Brenner, defined on the basis of smaller size, is doubtful, since Kemp found it falls within the size variation of *C. hughesii*. Another form which should be re-evaluated is the small, coarsely reticulate *"Peromonolites" reticulatus* Brenner, which, as Norris (1967) suggested, may be an angiosperm related to *Clavatipollenites* rather than a perinate spore (FIGS. 1j,k).

Brenner (1963) was skeptical about the angiospermous nature of *Clavatipollenites*, and he suggested that it represents an extinct group of gymnosperms. This possibility cannot be denied, but there is no concrete evidence for it, and it loses its force because definite (tricolpate) angiosperm pollen appears in the next formation, and all the morphological characters are quite at home among the angiosperms. Much of the range of variation (though not all the intermediates) may be found in the Chloranthaceae: *Ascarina* pollen resembles the fine clavate-retipilate forms, *Hedyosmum* the coarser clavate irregular-aperturate ones, while *Sarcandra* pollen is reticulate and nearly inaperturate. Similar retipilate sculpture is seen in the Myristicaceae and many dicots with tricolpate pollen, and variation in the aperture from monosulcate to trichotomosulcate is common in several monocot and "ranalean" families, e.g. Canellaceae (Wilson, 1964). In general, *Clavatipollenites* has more in common with the "ranalean" dicots than the monocots, which tend to have reticulate or tegillate rather than pilate exines.

If *Clavatipollenites* is tentatively regarded as of angiospermous origin, it is the oldest definite pollen record of angiosperms (cf. Couper, 1964). Older reports have gradually been rejected as more has been learned of Mesozoic gymnosperms. *Eucommiidites* has been discussed; the alleged nymphaeaceous pollen from the Scottish Middle Jurassic (Simpson, 1937) appears to have been grains of the coniferous genus *Zonalapollenites* and folded araucariaceous grains (Hughes & Couper, 1958), and Rouse's (1959) Upper Jurassic *Pterocarya* was a corroded *Classopollis* grain (Pocock & Jansonius, 1961). *Classopollis* itself was originally misinterpreted by Pflug (1953) as a tricolpate grain. A possible older occurrence of tricolporates, in the Berriasian-Valanginian of the Netherlands (Burger, 1966), has not yet been restudied.

The presence of primitive angiosperm pollen in the Patuxent-Arundel is consistent with the megafossil record. Fontaine (1889) described dicot leaves, *Ficophyllum*, *Rogersia*, and *Proteaephyllum* (in part), from the

Patuxent near Fredericksburg, Virginia. Palynological study of the matrix (Harvard University Paleobotanical Collections: cf. Fontaine, 1889, p. 5) shows that this locality is indeed of lower Potomac age. Berry (1911) questioned that these leaves were dicots and suggested that they could be *Gnetum*, but reinvestigation by Wolfe (pers. comm.) shows none of the distinctive fine venation or fiber network characters of *Gnetum*, and instead a series of presumed primitive angiosperm characters found in the living Winteraceae. It should be noted that the distinctive permanent tetrads of the Winteraceae are absent in the Potomac Group pollen flora, so a direct affinity is questionable. Isolated entire margined dicot leaves are also reported from the Aptian of the USSR (Vakhrameev, 1952).

No consistent way has been found to subdivide the Patuxent-Arundel palynologically, and Brenner (1963) included both in one biostratigraphic unit, Zone I. The age has not been defined more precisely than Barremian, Aptian, or early Albian. *Clavatipollenites* and ephedraceous pollen (Couper, 1964) and the schizaeaceous spore assemblage (Hughes, pers. comm.) indicate a post-Hauterivian age. The general assemblage suggests middle more than early Lower Cretaceous (cf. Pocock, 1962), and it is very much like the flora described from undifferentiated Aptian-Albian rocks of Portugal (Groot & Groot, 1962). Determinations of an early Neocomian age based on the megafossils (Berry, 1911; Dorf, 1952) were made when younger pre-Albian floras were practically unknown. The upper limit on the age is defined by the absence of tricolpate angiosperm pollen in the Patuxent-Arundel and its appearance at the base of the overlying Patapsco Formation. The appearance of tricolpates, discussed in the following section, is often taken to mark the Aptian-Albian boundary, but the sporadic record of Lower Albian tricolpates leaves open the possibility that the Arundel-Patapsco boundary lies within the Albian.

PATAPSCO FORMATION

Changes in the pteridophyte spore and gymnosperm pollen flora between the Arundel and the Patapsco are rather minor: the entrance of a handful of new species which Brenner (1963) used as index fossils for his Zone II, and the decline of some groups such as *Classopollis* and the Schizaeaceae within the Patapsco. The most important event is the appearance of small reticulate tricolpate grains. This pollen type is unlike the "pseudotricolpate" *Eucommiidites* type in having radial symmetry and a reticulate exine, and it is at present restricted to the dicots. In the lower part of the Patapsco (Brenner's Subzone A) the tricolpates are very uniform and present only in low percentages; in the upper part (Brenner's Subzone B, recognized by the entrance of several distinctive spores and gymnosperm pollen) they become more diverse and abundant; on rare occasions they constitute a majority of the pollen and spore flora. Their percentage variation from sample to sample (Brenner in fact encountered Subzone B assemblages with no tricolpates) suggests that they were restricted ecologically to certain habitats. *Clavatipollenites* also increases in abundance in the Patapsco; forms with irregular aperture morphology are not uncommon (FIGS. 1h,i).

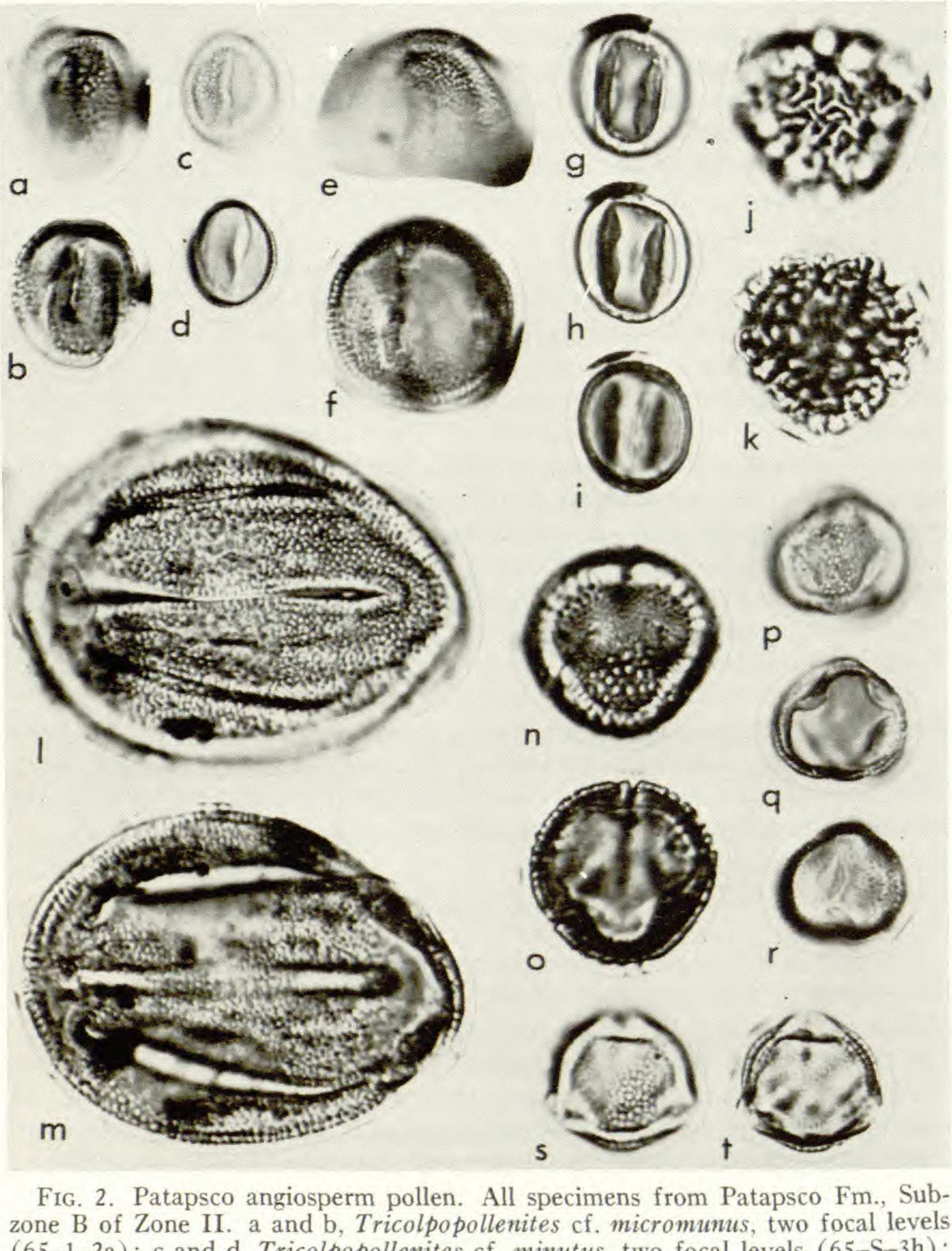

FIG. 2. Patapsco angiosperm pollen. All specimens from Patapsco Fm., Subzone B of Zone II. a and b, *Tricolpopollenites* cf. *micromunus*, two focal levels (65–1–2a); c and d, *Tricolpopollenites* cf. *minutus*, two focal levels (65–S–3h); e and f, Tricolpate type 1, pilate grain, two focal levels (65–1–2a); g, h, and i, Tricolpate type 2, nearly psilate grain, three focal levels (65–0–2g); j and k, "*Retitricolpites*" cf. *vermimurus*, polar view, two focal levels (65–2a–1a); l and m, *Tricolpopollenites* aff. *crassimurus*, two focal levels (65–2a–1b); n and o, Tricolpate type 3, reticulate, operculate grain, two focal levels (65–2a–1c); p, q, and r, Tricolporoidate type 1, grain with geniculate colpi, three focal levels (65–S–3i); s and t, Tricolporoidate type 2, oblate grain with subtriangular amb, two focal levels (65–2a–1j). All figures × 1000.

Patapsco tricolpate pollen shows some differentiation; at least in the upper part of the formation perhaps a dozen form species might be recognized. They are typically small (10–20μ), prolate or spheroidal in shape, with a fairly thin retipilate or reticulate exine, and colpi without any specialized margins or wide membranes. Many of the dominant forms (FIGS. 2a,b. Cf. *Tricolpopollenites micromunus* Groot & Penny, compared by Brenner to pollen of *Tetracentron*, or *Tricolpites albiensis* Kemp) have fine but well-defined retipilate or reticulate sculpture, without a continuous tegillum, and sexine somewhat thicker than nexine (1.0–1.5μ total exine thickness). *Tricolpopollenites minutus* Brenner is very small (11μ average axial dimension), with a reticulum which may be missed without oil immersion (FIGS. 2c,d). Besides these and similar microreticulate species, there are tricolpates with a *Clavatipollenites*-like exine, with free pila not arranged into a reticulum (FIGS. 2e,f), and at another extreme small forms with a nearly continuous smooth tegillum which were not reported by Brenner and are possibly restricted to the upper Patapsco (FIGS. 2g–i). Less common species are "*Retitricolpites*" *vermimurus* Brenner with a loose vermiculate reticulum (FIGS. 2j,k), and in the upper Patapsco large prolate tegillate grains close to *Tricolpopollenites crassimurus* Groot & Penny (FIGS. 2l,m), and a rather thick-walled spheroidal type with a coarse reticulum in the mesocolpia and internal thickenings (costae) at the margins of the operculate colpi (FIGS. 2n,o).

A previously unmentioned but possibly significant morphological feature of many of the Patapsco tricolpates, especially the *Tricolpopollenites micromunus* and *T. minutus* complexes, is a frequent buckling-out of the center of the colpi, giving them a geniculate appearance and suggesting a rudimentary os. This "tricolporoidate" tendency is prevalent in the upper Patapsco (FIGS. 2p–r). Another tendency, so far seen only in the upper Patapsco and later, results in oblate grains sub-triangular in equatorial outline, with the apertures at the protruding apices instead of sunken, as is the rule in Patapsco forms. These grains show differentiation of the nexine at the aperture and should probably be considered truly tricolporate (FIGS. 2s,t).

The appearance of tricolpate pollen seems to have been a major worldwide event, and in all areas which have been carefully studied there is a zone with small reticulate tricolpates but without triporates or typical tricolporates (cf. Krutzsch, 1963; Muller, 1968). This appearance generally may be dated as early or middle Albian, but refinement is needed in most areas. In England, the Patapsco-type *Tricolpites albiensis* Kemp appears at the base of the Middle Albian, but Kemp (1968) found rare grains of another tricolpate species in one Lower Albian sample. In western Canada tricolpates are reported by Norris (1967) from the base of the Colorado Group, which is considered basal Upper Albian (Norris) or late Middle Albian (Jeletzky, 1968) on the basis of ammonites, while they are reported to be absent from the underlying Mannville Group (Singh, 1964), which is presumably Middle Albian at the top. However, mid-Albian tricolpates cannot be ruled out here since the contact between the two groups is an unconformity, and in fact rare tricolpates occur locally in the upper Mannville (Pocock, pers. comm.; pers. obs.). The same relation holds in the U.S. Western Interior: tricolpates are present in the Thermopolis and Mowry shales of Colorado (lower Colorado Group equivalents; Tschudy & Veach, 1965), and in the Fall River Formation (basal Colorado Group equivalent) of the Black Hills, but they are absent from the underlying Lakota Formation (Cahoon, 1968). In Portugal, they occur in undifferentiated Albian but not in lower Aptian-Albian rocks (Groot & Groot, 1962); there are other reports from Albian rocks in France (Taugourdeau-Lantz & Jekhowsky, 1959), Germany (Krutzsch, 1963), and USSR (Zaklinskaya, 1961). In the central USSR Bolkhovitina (1953) reported tricolpates from the Lower Albian on; Yedemskaya (1960) found them in the Albian of the Caucasus, plus two isolated grains in the Aptian. In the Southern Hemisphere, tricolpates occur in the Upper Albian or Cenomanian of New Zealand (Couper, 1960), and in the Albian of northwestern Australia (Kemp, 1966).

In view of theories of a tropical origin of angiosperms, it would not be surprising to find earlier occurrences of angiosperm pollen or more pollen types in the present tropical areas. However, it appears that here, too, there is a zone with reticulate tricolpates and no triporates, and that the tricolpates do not appear demonstrably earlier than in present temperate areas. In North Borneo the Upper Albian or Cenomanian pollen flora contains angiosperms only of the same tricolpate and tricolporoidate types as in the Patapsco, associated with a very similar pteridophyte and gymnosperm flora (but lacking Pinaceae) (Muller, 1968). In northeast Brazil (Müller, 1966), the first angiosperm pollen is again reticulate tricolpates; the age is early Albian or possibly late Aptian. In higher zones (mid-Albian through Cenomanian, subdivision uncertain) these are joined by *Didymeles*-type tricolpodiorates and polyporates, and later triporates. In Upper Albian samples from Peru, Brenner (pers. comm.) found tricolpates and polyporates but no other angiosperm pollen. A very similar sequence occurs in Africa: in Senegal and the Ivory Coast reticulate tricolpates and tricolporates (tricolporoidates?) are the only angiosperms in the Lower (?) through much of the upper Albian; polyporates and later triporates enter higher in the Upper Albian-Lower Cenomanian interval (Vachey & Jardiné, 1962; Jardiné & Magloire, 1965). The Albian and Cenomanian of Gabon yield similar tricolpates, tricolpodiorates, triporates, and polyporates (Boltenhagen, 1965). The most unusual elements are the tricolpodiorates and polyporates. The latter are compared with the Amaranthaceae, but it should be noted that similar pollen occurs in some monocots (e.g. *Alisma* spp.). These pollen types do appear earlier in South America and Africa: the tricolpodiorates in fact are unreported elsewhere, but rare polyporates are known from the Cenomanian of Oklahoma (Hedlund, 1966) and Bohemia (Pacltová, 1966). Still, the record is consistent with a pre-Upper Albian interval with only tricolpate and tricolporoidate angiosperms.

Brenner (1963) considered the Patapsco to be Albian, and the record of the first tricolpates as reviewed here indicates that it is almost certainly no older than Lower Albian and may in fact be younger. Considering the record in England and the North American Western Interior, it is quite possible, as suggested by Wolfe and Pakiser (ms.), that the underlying Patuxent and Arundel are largely Lower Albian in age. More work on the pollen flora near the Aptian-Albian boundary in well-dated sequences (e.g., in Texas) is clearly in order.

Aside from the Fredericksburg material mentioned above, the first angiosperm leaves in the Atlantic Coastal Plain are found in the Patapsco (Fontaine, 1889; Berry, 1911), where they are still a subordinate element. Similar fossils occur in the (Middle?) Albian lower Blairmore flora of western Canada (Bell, 1956), the Cheyenne Sandstone of Kansas (Berry, 1922), deposits in the Kolyma basin in eastern Siberia (Samylina, 1960), Lower and Middle Albian rocks of Kazakhstan (Vakhrameev, 1952), and the Albian of Portugal (Teixeira, 1948); Vakhrameev (1952) and Takhtajan (1960) have noted the characteristic small size of these Albian leaves and suggested a relation to a still unperfected conductive system.

Brenner (1963) proposed an Upper Albian age for the upper Patapsco (Subzone B) on the basis of a close specific similarity to the Upper Albian-Lower Cenomanian angiosperm pollen flora of Portugal (Groot & Groot, 1962). It is generally in the Upper Albian that tricolpate pollen becomes a characteristic though still subordinate element in the flora and attains a certain low degree of diversity. Similar Upper Albian (-Lower Cenomanian?) floras are seen in the lower Colorado Group of western Canada (Norris, 1967), the Thermopolis and Mowry shales of Colorado (Tschudy & Veach, 1965), and Upper Albian-Lower Cenomanian strata in the USSR (Bolkhovitina, 1953; Bolkhovitina *et al.*, 1963). At the present time it is impossible to rule out a Lower Cenomanian age for part of Subzone B, considering the uncertain dating of the correlative deposits, the general lack of well-dated Lower Cenomanian pollen for comparison, and the only slightly more modernized floras of the Middle Cenomanian (cf. Hedlund, 1966, and below).

It is in the Upper Albian and Lower Cenomanian that we see the first megafossil floras dominated by dicot leaves. Such floras are the Dakota flora of Kansas (Lesquereux, 1892), long considered Upper Cretaceous but now known to be in part correlative with the Upper Albian Mowry Shale, the upper Blairmore flora of western Canada (Bell, 1956), and a series of Upper Albian floras from Kazakhstan (Vakhrameev, 1952). Characteristic for these floras are a variety of entire leaves and a large number of lobate leaves with platanaceous venation which have been referred to several unrelated modern genera (*Aralia*, *Sassafras*, *Sterculia*, *Liquidambar*). A "Dakota" flora has not been described from the Patapsco, but this may be because the early collections were made mostly near the Potomac River, where the Patapsco appears to be pinching out; I have seen upper Patapsco localities (65–2a, 65–S) rich in simple entire marginal leaves of a type not described by Berry (1911).

RARITAN FORMATION

The basal Coastal Plain unit in New Jersey, the Raritan Formation, has not been studied as comprehensively as the Potomac Group. The Woodbridge Clay member, near the base of the formation in the Raritan Bay area, is best known palynologically (Groot, Penny, & Groot, 1961; Kimyai, 1966; Wolfe & Pakiser, ms.). This unit, dated as Middle or Upper Cenomanian by marine fossils, is significantly younger than the typical Patapsco of Maryland: the angiosperm pollen is much more diverse, with several definite tricolporates (the dominant pollen type in modern dicots) and low percentages of the first triporates, the genera *Complexiopollis* Krutzsch and *Atlantopollis* Krutzsch of the Normapolles group of Pflug (1953). Older beds which promise to close the gap between the Patapsco and Raritan are becoming known to the south of Raritan Bay and in the subsurface, as are younger beds of presumed Turonian age (the South Amboy Fire Clay member) in the Raritan Bay area.

The Raritan is the first Coastal Plain unit in which angiosperms clearly dominate the pollen flora, but gymnosperms and pteridophytes are still important elements. These are mostly Pinaceae, Podocarpaceae (including *Phyllocladus*-like forms and perhaps the bizarre genus *Rugubivesiculites* Pierce, with a ruffled central body, which appears in the upper Patapsco but is most typical of the North American Upper Cretaceous), Taxodiaceae, Cupressaceae, Araucariaceae, Cyatheaceae, and Gleicheniaceae; the Schizaeaceae are in decline, and most of the extinct groups represented by *Classopollis*, *Eucommiidites*, *Vitreisporites*, etc. are very rarely seen. The angiosperm pollen of the Woodbridge includes reticulate tricolpates of the Albian type, though many appear to be new species, and occasional monosulcates (*Clavatipollenites*, *Liliacidites*). A larger portion is assumed by small psilate tricolpates and tricolporates (FIGS. 3a–d). Some of the most characteristic of these continue a trend seen in the upper Patapsco: they are oblate and triangular in equatorial outline, with apical apertures (FIGS. 3e,f. Cf. *Tricolporopollenites triangulus* Groot, Penny, & Groot). Besides these small, simple tricolpates and tricolporates, there are larger forms with more complex exine structure (reticulate to completely tegillate) and apertures (e.g., FIGS. 3g–i). An unusual new pollen type is represented by two forms with permanent tetrads: one is larger, with a smooth tegillum supported by large pila, and with somewhat obscure colpi arranged according to Fischer's law (FIGS. 3j,k); the other is smaller, psilate to retipilate, with very irregular colpoid areas (FIGS. 3l,m). Neither is like the familiar tetrads of the Ericaceae; the smaller type is strikingly similar to pollen of the monogeneric family Myrothamnaceae of South Africa and Madagascar.

The most striking new element is the first of the bizarre triporate Normapolles, which are dominant in the Upper Cretaceous and earliest Tertiary of Europe. They are an extinct group, not directly comparable to any living angiosperms, though if the complex protruding apertures of some of the later form genera were reduced somewhat and the grains became less triangular, they might approach pollen of some modern amentiferous

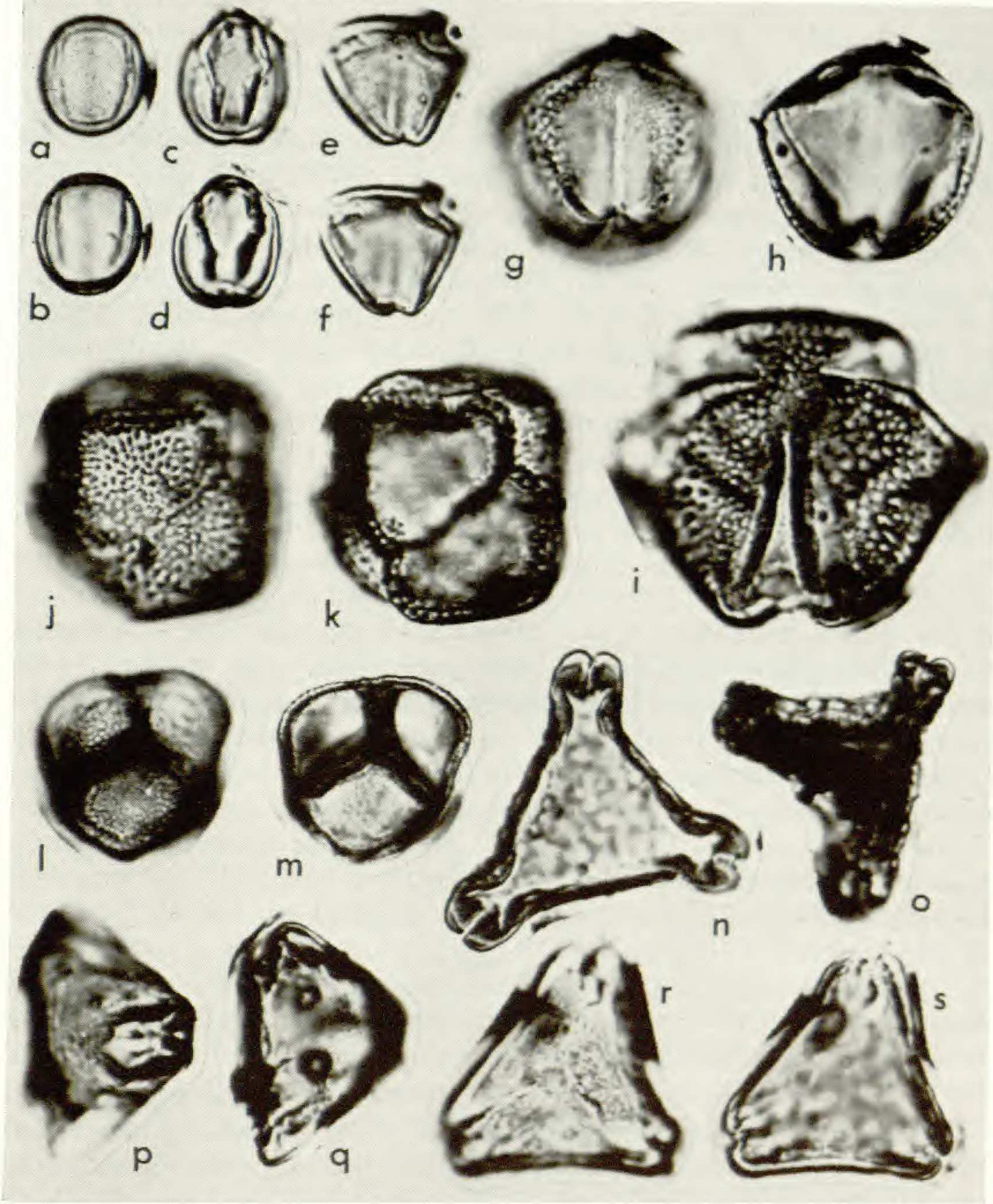

FIG. 3. Lower Raritan and Patapsco-Raritan transition zone angiosperm pollen. All specimens except p–s from Woodbridge Clay member, Raritan Fm. a and b, Tricolpate type 4, prolate, psilate grain, two focal levels (68–10–1b); c and d, Tricolporate type 1, prolate, psilate grain, two focal levels (68–8–1a); e and f, *Tricolporopollenites* cf. *triangulus*, two focal levels (68–10–1b); g and h, Tricolporate type 2, reticulate grain with flat mesocolpia, two focal levels (NJ 2–1a); i, Tricolporate type 3, reticulate grain with marginate colpi (68–8–1a); j and k, Tetrad type 1, large, tegillate grain, two focal levels (NJ 2–1a); l and m, Tetrad type 2, small, retipilate grain, two focal levels (68–10–1c); n, *Complexiopollis* sp. (NJ 2–1b); o: *Atlantopollis* sp. (68–10–1b); p and q, Tricolporate type 4, possible precursor of Normapolles group, oblique view, two focal levels (TR(1551–3)–1c: upper part of Patapsco-Raritan transition zone); r and s, same, polar view, two focal levels (TR(1551–3)–1c). All figures × 1000.

groups (Betulaceae, Casuarinaceae, Myricaceae, Rhoipteleaceae, Juglandaceae, Urticales). In fact, as was pointed out by Góczán *et al.* (1967) in their revision of the group, they cannot be rigidly separated from the Tertiary "Postnormapolles" of Pflug (1953), which include many of the modern "Amentiferae." *Complexiopollis* and *Atlantopollis* are among the oldest Normapolles in Europe. *Atlantopollis* differs from the psilate or scabrate *Complexiopollis* in its coarsely reticulate or (in New Jersey) verrucate sculpture. Apertures in both genera are very short colpi or elongate pores, with the nexine differentiated into an endannular collar just inside the pore (FIGS. 3n,o). The multiple endannular rings seen in European Turonian species and in the upper Raritan (FIG. 4a) are poorly developed in lower Raritan forms.

The Normapolles and other pollen and spores provide an age determination consistent with that from the marine fauna of the Woodbridge. A Normapolles assemblage with only *Complexiopollis* and its relatives was first described from the Lower Turonian of Germany (Krutzsch, 1959), but it has been extended an uncertain distance down into the Cenomanian. The Cenomanian Peruc Formation of Bohemia (Pacltová, 1966; Pacltová & Mazancova, 1966) is probably closest to the Woodbridge: very similar Normapolles are present in very low proportions, while the rest of the angiosperm flora contains reticulate and psilate tricolpates and tricolporates, including a triangular form of the *Tricolporopollenites triangulus* type (but also polyporates unknown in the Raritan). Cenomanian deposits of Portugal (Groot & Groot, 1962) also contain *Complexiopollis* and *Atlantopollis* (as *Latipollis*). In North America, the Tuscaloosa Group of Alabama, believed to be of late Cenomanian age, yields a flora with *Complexiopollis* and *Atlantopollis* almost identical to that of the Woodbridge (Leopold & Pakiser, 1964). *Complexiopollis* (as *Punctatricolporites*) appears near the putative Cenomanian-Turonian boundary in the Eagle Ford Shale of Texas (Brown & Pierce, 1962). Wolfe and Pakiser (ms.) believe the Woodbridge is Upper Cenomanian, and considering the low percentages of Normapolles this is probably correct, though the range data permit a Lower Turonian age as well. It is probably younger than most of the Middle Cenomanian, since Normapolles are not reported from the Middle Cenomanian Woodbine Formation of Oklahoma (Hedlund, 1966), nor the "Dakota Group" of Minnesota (Pierce, 1959), though both these floras have post-Patapsco elements such as psilate tricolporates and similar conifers (diverse *Phyllocladus*-type and *Rugubivesiculites*) and spores (common large *Sphagnumsporites, Camarozonosporites,* and *Gleicheniidites*).

Triporates other than Normapolles appear in other parts of the world probably in the Cenomanian, though the age control is lamentably poor. Thus in North Borneo grains with simple round pores appear in a zone loosely dated as Cenomanian to Senonian (Muller, 1968); triporates compared with Sapindaceae or Proteaceae appear near the end of an Upper Albian to Lower Cenomanian interval in Senegal and the Ivory Coast

(Jardiné & Magloire, 1965) and late in the Upper Albian through Cenomanian interval in northeast Brazil (Müller, 1966).

It is becoming clear that there was an interval in the Atlantic Coastal Plain after the typical Patapsco and before the Woodbridge with angiosperm floras including tricolporates, many psilate and some triangular, but without Normapolles. Extinct gymnosperms such as *Classopollis* are often common in these floras. This Patapsco-Raritan transition zone is seen in surface samples from Elk Neck in northern Maryland and near Trenton, New Jersey (Wolfe & Pakiser, ms.), from the uppermost "Raritan" of Bodkin Point, Maryland (pers. obs.), in the subsurface "Raritan" near Delaware City, Delaware (Brenner, 1967), at the top of the "Raritan(?)-Patapsco" in a well near Waldorf, Maryland, and in a well some thirty miles downdip from the Raritan Bay outcrop area on the Toms River, New Jersey (pers. obs.). The data of Wolfe and Pakiser and from the Toms River well suggest that the first "Raritan" elements to appear are the more prolate psilate tricolporates and, soon after, the triangular forms; other "Raritan" elements enter as Lower Cretaceous gymnosperms and ferns decline, until the flora is very close to the Woodbridge except for the absence of Normapolles.

In one of the uppermost pre-Woodbridge samples from the Toms River well, an unusual tricolporate occurs with a shape and sculpture very much like *Complexiopollis* but with longer vestigial colpi and no typical annulus or endannulus. The apertures approach those of some of the more complex Raritan triangular tricolporates, suggesting a link between less bizarre tricolporates and the Normapolles (Figs. 3p–s).

Wolfe and Pakiser (ms.) characterize the pollen flora of the South Amboy Clay member as essentially the same as the Woodbridge flora except for some new non-Normapolles triaperturates. However, samples from four localities in the upper Raritan, including the classic Kreischerville collections of Hollick (New York Botanical Garden Paleobotanical Collections: cf. Hollick & Jeffrey, 1909), yield floras which appear to be significantly younger than the Woodbridge. Although many of the Normapolles might be considered advanced members of the *Complexiopollis* group (Fig. 4a), most show characters of the mid-Turonian and younger *Plicapollis* and *Vacuopollis* groups. Intergradations render generic separation difficult, but the genus *Pseudoplicapollis* Krutzsch, with rudimentary endoplicae and a characteristic pore structure, is definitely present (Fig. 4b). In most of the grains the apertures tend to protrude less than in *Complexiopollis* and consist of nearly round pores, with the nexinous collar retracted or reduced to produce a true vestibulum (as in *Plicapollis* Pflug) or atrium (as in *Vacuopollis* Pflug). Many show apparently structural folds (Figs. 4c,d), though these are generally less regular than the "endoplicae" of typical (younger?) *Plicapollis*. Some of the subspheroidal forms approach the myricoid genus *Triatriopollenites* Thomson & Pflug (Fig. 4g). Also present are small psilate triporates perhaps unrelated to the Normapolles (Figs. 4e,f), and large, oblate brevitricolporates (*Porocolpopollenites, sensu* Leopold & Pakiser 1964: Fig. 4h). Other new tricol-

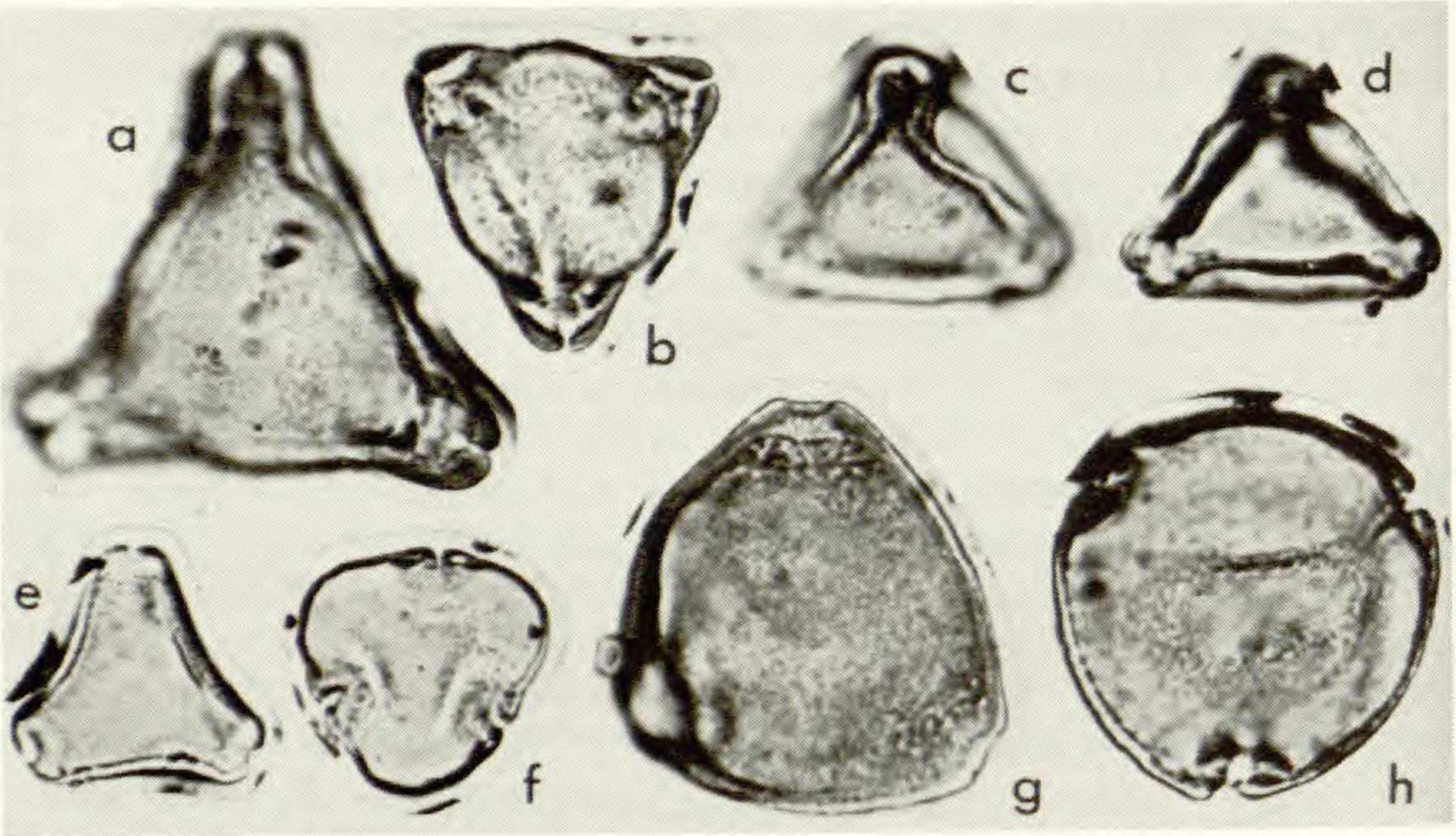

FIG. 4. Upper Raritan angiosperm pollen. a, *Complexiopollis* sp. (68–23–1a: South Amboy Fire Clay member); b, *Pseudoplicapollis* sp. (68–26–1a: South Amboy Fire Clay or Old Bridge Sand member); c and d, aff. *Plicapollis* sp., two focal levels (68–25–1a: South Amboy Fire Clay member); e, Triporate type 1 (68–23–1b: South Amboy Fire Clay member); f, Triporate type 2 (68–26–1b: South Amboy Fire Clay or Old Bridge Sand member); g, aff. *Triatriopollenites* sp. (68–25–1b: South Amboy Fire Clay member); h, *Porocolpopollenites* sp. (*sensu* Leopold & Pakiser) (68–25–1c: South Amboy Fire Clay member). All figures × 1000.

porates appear to be forerunners of typical Magothy species (cf. FIGS. 5h–k). Most of these forms are reported from the McShan and Eutaw formations of Alabama (Leopold & Pakiser, 1964), which are referred to the later Turonian by Wolfe and Pakiser (ms.). Although strictly comparable floras have not been described from Europe, the range data of Góczán *et al.* (1967) suggest a Middle or Upper Turonian age.

MAGOTHY FORMATION

The Magothy Formation, which extends from Maryland through Long Island, has a highly diversified angiosperm flora which has been described by Stover (1964), Groot, Penny, and Groot (1961), and more completely by Wolfe and Pakiser (ms.). As noted by Wolfe and Pakiser, the rich and advanced Normapolles element indicates a sizable break in deposition before Magothy time, though the presence of Turonian in the Raritan may close some of the gap. The Raritan marks the end of the nearly continuous mid-Cretaceous record; remarks on the Magothy flora will hence be only of a general nature.

Normapolles are a dominant element, represented by at least a dozen genera. The *Plicapollis-Pseudoplicapollis* group (with Y-shaped thickenings and vestibula), the *Vacuopollis* group, now represented by typical

Vacuopollis (with large atria and thick annuli made up of minute inward projecting rods), and *Trudopollis* Pflug (with thick annuli and endannuli and a space or interloculum between inner and outer exine) are especially common (FIGS. 5a–d). There are many small Normapolles (*Minorpollis*, etc.) and other simple triporates of the type seen in the upper Raritan (FIG. 5e; cf. FIGS. 4e,f). Such an assemblage must be at least as young

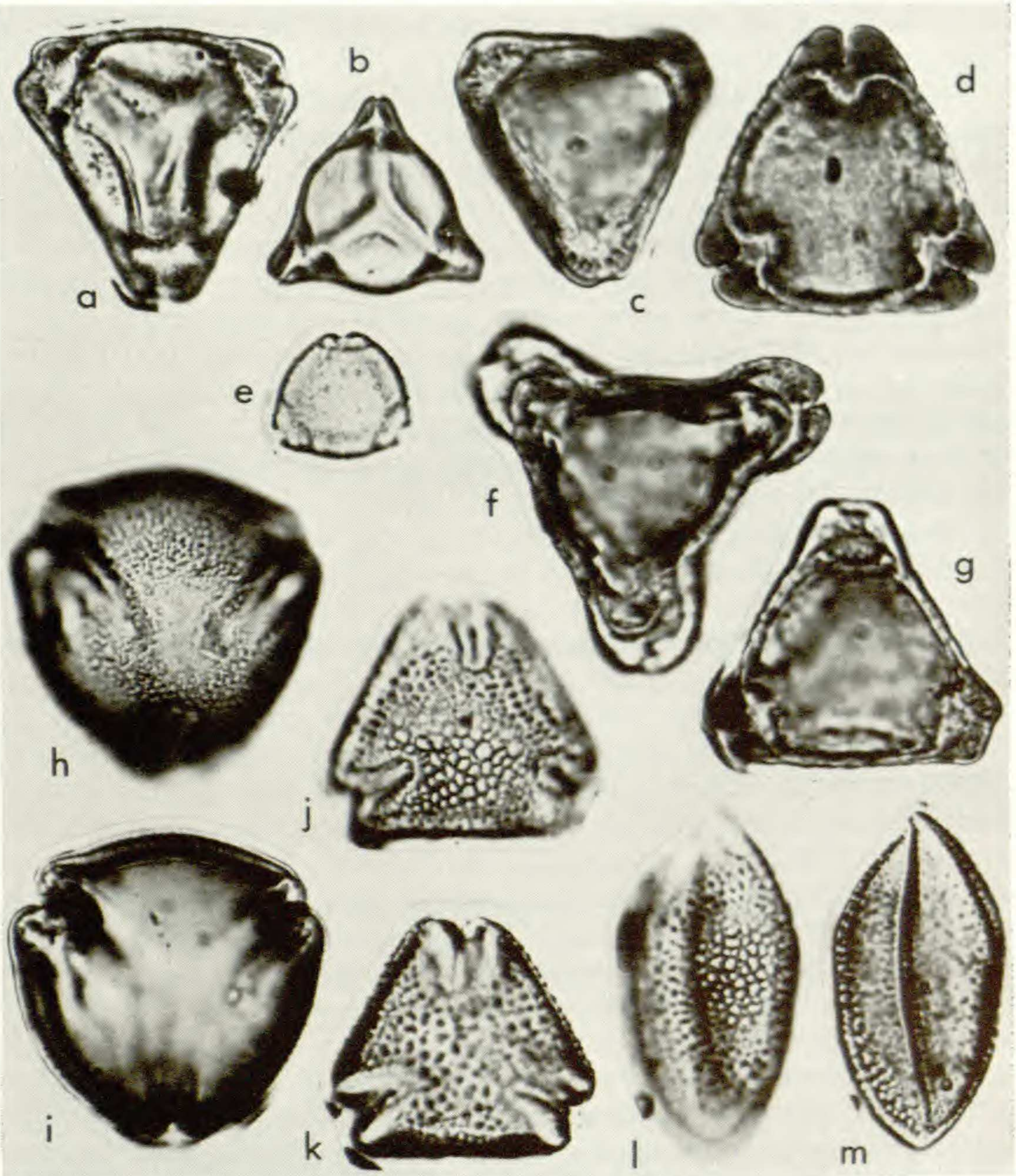

FIG. 5. Magothy angiosperm pollen. a, *Plicapollis* sp. (68–14–1a: Amboy Stoneware Clay member); b, *Pseudoplicapollis* sp. (68–14–1a); c, *Vacuopollis* sp. (68–14–1a); d, *Trudopollis* sp. (68–14–1a); e, Triporate type 3 (68–14–1a); f, aff. *Praebasopollis* sp. (68–14–1a); g, aff. *Pecakipollis* sp. (68–14–1a); h and i, Tricolporate type 5, two focal levels (68–16–1a: Cliffwood beds); j and k, Tricolporate type 6, two focal levels (68–16–1a); l and m, Monosulcate type 1, grain with sulcus on lower side, two focal levels (Ch-Bf 127(441–2)–1b: Magothy Fm. undifferentiated). All figures × 1000.

as mid-Coniacian (cf. Góczán *et al.*, 1967) and is probably younger, since most of these genera become abundant only in the Santonian (Krutzsch, 1957). More specific evidence is provided by close relatives or new species of the mid-Santonian and younger genera *Praebasopollis* Groot & Krutzsch (with two endannular lips extending into the large vestibula: FIG. 5f) and *Pecakipollis* Krutzsch & Pacltová (*Plicapollis*-like grains without clear endoplicae and with some *Trudopollis* traits: FIG. 5g). A Santonian age is verified by a late Santonian ammonite found in the upper Magothy of New Jersey (Sohl, pers. comm.).

Tricolpates and tricolporates, many continuing from the upper Raritan, are highly diverse in the Magothy. Upper Raritan and Magothy pollen types commonly suggest modern families, but most species have anomalous features or characters now found only in related families. Thus the grain in FIGURES 5h and i has some nyssaceous and cornaceous characters but would not be at home in either family, while the grain in FIGURES 5j and k has rhamnaceous apertures but hippocrateaceous or celastraceous sculpture, and the common myricoid grains (cf. FIG. 4g) have more of an endannulus than modern Myricaceae. Reticulate, psilate, and spiny monosulcates very suggestive of modern palms are abundant in some samples (FIGS. 5l,m). Palm megafossils, among the oldest known, are also found in the Magothy (Berry, 1916).

From the Turonian on, the world pollen flora is marked by provincialism which contrasts strongly with the cosmopolitanism of the early Cretaceous. Zaklinskaya (1962) first pointed out the major provinces of the Northern Hemisphere in the Senonian and Maestrichtian: the *Aquilapollenites* province in Siberia and western North America and the Normapolles province in Europe and eastern North America (cf. Góczán *et al.*, 1967). *Aquilapollenites* Rouse is a peculiar extinct form with a prolate, often heteropolar, central body and protruding arms bearing the apertures. It is often associated with pollen of possible proteaceous affinities which is common also in the Senonian of New Zealand, Australia, and Africa. *Aquilapollenites* has been found in equatorial Africa (Jardiné & Magloire, 1965) and Borneo (Muller, 1968), but not in the Normapolles province until the breakdown of provincialism in the Paleocene, when it occurs briefly in the Gulf Coastal Plain (Tschudy, pers. comm.). Normapolles are unknown in Africa and Borneo and very rare in Siberia. There are also strong similarities between the pollen floras of Africa and Brazil in the Upper Cretaceous, but these have not been studied as well (cf. Müller, 1966). The peculiar distribution of the Northern Hemisphere provinces is clearly a reflection of the epicontinental seas which extended from the Gulf of Mexico to the Arctic Ocean and along the east side of the Urals (cf. Tschudy, 1966).

The Magothy flora is a representative of the Normapolles province, but it illustrates that the province should be divided into American and European areas. Though many of the stratigraphically important genera and groups of genera are common to Europe, Wolfe and Pakiser (ms.)

point out that many bizarre forms are restricted to Europe, and many of the Magothy genera are new, being most nearly represented only by relatives in Europe. They note that the *Trudopollis* group is absent from the American Turonian, and that most of the Magothy dicots other than Normapolles are still unreported from Europe. The Atlantic Ocean certainly acted as a barrier to migration in the Senonian, but it is still surprising that it may have been less effective than the epicontinental sea of the American interior.

GENERAL EVOLUTIONARY IMPLICATIONS

In the late Lower Cretaceous the angiosperms are a very subordinate, undiversified element in the pollen flora; by the mid-Upper Cretaceous they are dominant and highly differentiated, though far from modern in total variation. The increase in diversity is regular, with new morphological types appearing not at random but in what can be read as series that permit derivation of each type from an earlier one. Small retipilate monosulcates are joined by small retipilate tricolpates; these pass into tricolporoidates and then tricolporates of more diverse exine structure, and these into the first triporates, which in turn diversify. The pollen record by itself leads unambiguously to the conclusion that we are witnessing a major adaptive radiation of a new group. Since we have the time dimension, we can tell which way to read our series and hence determine which character states are primitive (i.e. ancestral) and which advanced (i.e. derived). The resulting trends of course apply directly only to the plants of the time observed, and many of them have doubtless been reversed in later evolution, but they are relevant to modern groups insofar as the present major alliances are the result of this radiation and much of the ancient range in morphology is retained today. Likewise, we observe directly only evolution in pollen morphology, but this tells us something about general phylogeny insofar as pollen morphology is useful in recognizing taxa today, and as primitive or advanced characters in different organs are loosely correlated as a result of lesser or greater evolutionary rates in a given line (cf. Sporne, 1954).

The pollen record sets some limits on the time and place of origin of the angiosperms. The group must have originated at the beginning of the observed radiation (in the Barremian-Aptian) or earlier, though the possibility that the earliest pollen with angiosperm characters (*Clavatipollenites* and the early Albian tricolpates) was produced by plants which had not reached the angiosperm level in other organs should not be ignored. But at least in the Aptian, the typical dicotyledonous leaf morphology had been attained as well.

So far, the pollen record provides no conclusive evidence on the hypothesis that the angiosperms appeared and diversified first in the tropics. The earliest tricolpates there are similar to those in the temperate zones, though after the Middle Albian some pollen types seem to have appeared earlier in the tropics. There is suggestion of a lag of a third of a stage in invasion of the middle latitudes in reports of Lower Albian and even Aptian tricolpates in Africa and South America on the one hand and their poor record before the Middle Albian in England and North America on the other, but the stratigraphy requires much refinement before this can be considered established. In any case, the tropical belt in the early Cretaceous undoubtedly covered areas which are now temperate. The tree ferns and cycads in the Potomac Group suggest at least an equable (warm temperate?) climate, though the lack of bisaccate conifers in the tropics indicates some latitudinal differentiation.

One area that is ruled out as a center of angiosperm origin and evolution is the Arctic. Megafossil and microfossil floras from northern Siberia and Alaska north of the Brooks Range rarely contain angiosperms until well into the Cenomanian (Teslenko, 1958; Vasilievskaya, 1956; Smiley, 1966; Stanley, 1967; cf. Hughes, 1961b). Most of Seward's Lower Cretaceous angiosperm leaves from the Kome flora of Greenland appear to have come from the Upper Cretaceous, and the status of the one remaining leaf is uncertain (Koch, 1964).

It is certainly possible that primitive, undiversified angiosperms existed as a subordinate part of the flora long before the Barremian. We need only compare the mammals, which originated in the late Triassic but did not undergo major radiation until the Tertiary. Rare angiosperms with cycad-like pollen, as in several "ranalean" families, might easily go unnoticed in the Jurassic or Triassic. However, theories that postulate that the angiosperms not only existed but diversified long before the Cretaceous in isolated areas such as the tropical uplands (e.g. Axelrod, 1952) and simply migrated into other areas in the Cretaceous do become implausible in the light of the progressive appearance of morphological types. While we might expect a gradual increase in the number of types as a result of such migration, we would expect a sequence of unrelated derived types rather than convincing evolutionary series.

The record of early angiosperms is doubtless biased toward prolific pollen shedders and wind-pollinated offshoots. Even so, if much more highly evolved pollen was being produced by strictly insect-pollinated plants, we would expect to see it occasionally. Isolated large, more highly sculptured grains often found in the Potomac Group (e.g. "*Retitricolpites" geranioides* (Couper) Brenner or the form in FIGS. 21,m) may in fact represent such plants, but they are similar morphologically to their smaller and more common associates. The simplest assumption, that the pollen we see preserved is fairly representative of the morphological types that existed at the time, is followed here.

The concept of an evolutionary radiation of angiosperms beginning in the early Cretaceous may appear to be in conflict with the megafossil record. Lower Cretaceous leaves have been placed in such unrelated modern genera as *Populus* and *Sassafras* and form genera (e.g. *Ficophyllum* and *Celastrophyllum*) intended to suggest families as distant as Moraceae and Celastraceae. To reconcile such diversity with the uniformity of the pollen flora by postulating that pollen evolution lagged behind while other organs differentiated to nearly a modern level would require an incredible amount of mosaic evolution in many lines. The pattern of variation in modern angiosperms suggests rather that, in general, pollen morphology has not behaved markedly unlike other character complexes: families may be either very uniform or diverse palynologically. What is needed is a re-evaluation of the leaf determinations, which were made without modern techniques of cuticle and fine venation analysis and apparently without the caution required in studying evolutionarily important fossils. Pacltová (1961) found that cuticles of "*Eucalyptus*" from the Cenomanian of Bohemia bore no specific relation to that genus; the platanaceous venation of Dakota leaves placed in several unrelated genera and Wolfe's case for the winteraceous affinity of *Ficophyllum* have been mentioned. A detailed study of the morphology of Cretaceous leaves might prove of more evolutionary interest than attempts at identification of taxa.

SPECIFIC TRENDS

The most striking evolutionary trends seen in early angiosperm pollen are in the apertures and shape of the grains. Other more questionable trends involve the exine sculpture and size. These trends are summarized in TABLE 3 (p. 28).

It would appear that the monosulcate condition of *Clavatipollenites*, the first convincing angiosperm pollen, is very primitive. Within this group we see as later variants trichotomosulcates, inaperturates, and grains with several ill-defined colpoid areas. There is a definite trend to fusion of structural elements into a true reticulum, as in *Liliacidites*.

The record is consistent with derivation of the tricolpates, the next most ancient major pollen type, from monosulcates of the *Clavatipollenites* type. The similar retipilate exine structure in *Clavatipollenites* and the earliest tricolpates favors this hypothesis over such alternatives as a completely independent origin or derivation from the *Eucommiidites* type. It is a general principle that in seeking ancestors for a group we should consider its most primitive (here earliest) members rather than advanced (later) forms (Thorne, 1963). There are, unfortunately, no obvious intermediates between monosulcates and tricolpates in the Cretaceous record, but the presence of trichotomosulcate apertures and irregular colpoids in *Clavatipollenites* may be significant. A theory of the origin of the tricolpate condition by loss of the polar connection of the three arms in a trichotomosulcate grain has been advanced by Wilson (1964). However, intermediate forms with three colpi displaced toward the pole are lacking. Another possibility is that the tricolpate condition represents the stabilization of an irregular situation with several colpoids. In the Chloranthaceae a similar process may have produced the longitudinal colpi (usually six) in *Chloranthus*.[2]

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[2] See footnote 1 on page 6.

Within the triaperturate group trends are more readily documented, and the wealth of intermediates leaves no need to invoke independent origin of the more complex forms. Tricolporates may have originated from tricolpates via tricolporoidates with only a slight weakening at the center of the colpus membrane. In some lines this trend was associated with a change in shape from prolate or spheroidal to oblate with a triangular amb and apical apertures. A pervasive trend in all the triaperturate classes (as well as the monosulcates), but most common in the tricolporates, was the fusion of exine structural elements into a complete tegillum, often resulting in psilate grains. Permanent tetrads also appear as a later offshoot in the triaperturate groups.

The small size of the early tricolpates suggests that this may be a primitive character in the triaperturates. However, the occasional presence of large grains suggests size was an unstable trait from the beginning, being subject to changes in pollination ecology. Small grains are often associated with wind pollination, but the Albian forms are even smaller than most amentiferous pollen. A comprehensive comparative study of size-pollination relations in modern angiosperm pollen would be desirable.

The culmination of the trend toward apical apertures is evidently seen in the triporate Normapolles, which may have been derived from conventional dicots through triangular tricolporates in pre-Woodbridge time. The Normapolles show various peculiar trends, such as the evolution of atria, vestibula, and other elaborations of the pores, and the development of endoplicae suggesting the arci of the Betulaceae, Rhoipteleaceae, and Ulmaceae. Soon after the origin of the group, the shape trend was apparently reversed to produce subspheroidal grains, as in most of the modern "Amentiferae." Other triporates, seen in the upper Raritan and parts of the world where Normapolles are lacking, may be of independent origin; they might originate by reduction of the colpus in a tricolporate grain or perhaps by contraction of the colpus in a tricolpate.

Pollen with numerous scattered pores occurs in the Cretaceous of some areas, apparently always after the entrance of tricolpates. Polyporates are found today in both monocots and dicots: the fossil record is consistent with derivation from either monosulcates or tricolpates and does not indicate which alternative is correct. Occasional dicolpate and polycolpate variants of tricolpate Raritan species and tetraporate Normapolles grains are within the normal variation of modern species; apparently such variation did not lead to major trends in the Cretaceous.

The proposed evolutionary relationships among the major pollen types are shown in their stratigraphic framework in FIGURE 6. This scheme is almost identical to the one proposed by Takhtajan (1959, 1966), based on the comparison of the pollen of angiosperms which are believed to be primitive or advanced in other characters. Many of the same trends are implicit in the writings of Bailey and coworkers (e.g. Money, Bailey, & Swamy, 1950) and of Wodehouse (1936). One of Takhtajan's important trends, from monosulcate to monoporate, is not shown since mono-

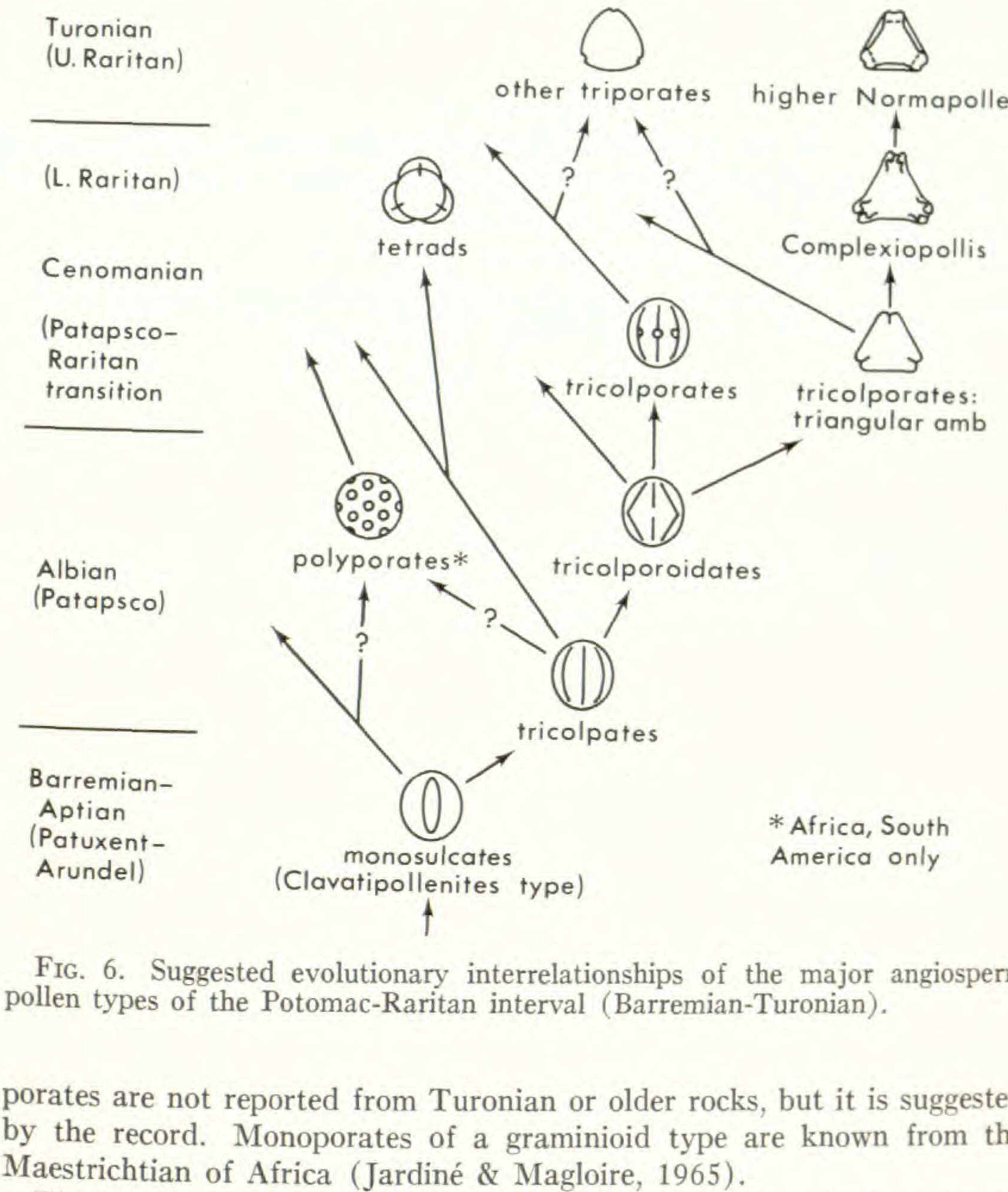

FIG. 6. Suggested evolutionary interrelationships of the major angiosperm pollen types of the Potomac-Raritan interval (Barremian-Turonian).

porates are not reported from Turonian or older rocks, but it is suggested by the record. Monoporates of a graminioid type are known from the Maestrichtian of Africa (Jardiné & Magloire, 1965).

The trends proposed here are very different from those of Kuprianova (1966), who lists as primitive a large number of characters found in such groups as the Santalales, many amentiferous plants, and Upper Cretaceous fossils including the Normapolles which suggest an ancestry with trilete spores. This approach overlooks earlier Cretaceous fossils which point toward simple tricolpate or monosulcate ancestral forms; the fossil sequence clearly shows sporelike Upper Cretaceous forms and their modern analogs are secondarily derived. As a rule, I would suggest that no exclusively post-Middle Albian pollen types can be used directly to reconstruct primitive conditions in angiosperms.

PHYLOGENETIC INFERENCES

Although the Cretaceous pollen record does not show us the origin of the angiosperms, it does allow us to make more secure inferences about the ancestors of the group. Thus the earliest monosulcate angiosperm pollen points to a group of gymnosperms with monosulcate pollen. This suggests an ancestor among the cycadopsids (i.e. the seed ferns and their presumed derivatives) rather than the coniferopsids or pteridophytes. An ultimate seed fern ancestor, making the angiosperms a parallel group to the cycads, Bennettitales, and Caytoniales, is suggested by the comparative morphology of the other plant organs (cf. Takhtajan, 1960; Cronquist, 1968). Clearly more must be known of Triassic, Jurassic, and, as Hughes (1961b) emphasizes, Lower Cretaceous gymnosperms before a more definite hypothesis may be presented.

Discussion of an ancestor of the angiosperms assumes the group is monophyletic, at least in the loose sense of Simpson (cf. Cronquist, 1968). This assumption is consistent with the record, which appears to show one major radiation, with the more ancient representatives of putative lines more instead of less similar to each other. Even the Normapolles may be derived from earlier tricolporates. This argument holds only for the basically tricolpate groups and their immediate monosulcate ancestors (i.e. the bulk of the dicots), and it does not mean all the characters we associate with the angiosperm grade had evolved when the taxon originated. In any case, it is quite likely that still more primitive groups with monosulcate pollen reached the angiosperm level in several lines, resulting in much of the heterogeneity of the living "Ranales."

Speculation on the affinities of early angiosperm pollen might easily lead to unwarranted conclusions on the age of modern taxa. It is not difficult to find modern analogs of Albian pollen: we have seen that much of the morphological variation in the *Clavatipollenites* type may be found in the Chloranthaceae, while similar generalized tricolpates occur in the Lardizabalaceae and Menispermaceae, or the Tetracentraceae, Hamamelidaceae, Platanaceae, and related families of the Trochodendrales and Hamamelidales of Cronquist (1968). However, the monosulcate and tricolpate complexes were young and evolving rapidly in the Albian, and their total diversity could probably be accommodated in two or three closely related orders and perhaps five to ten families. In contrast, the modern families mentioned are relictual and isolated from each other by specialization and extinction. It would probably be a mistake to believe the similarities indicate any more than that such taxa have retained a primitive pollen type, and hence perhaps other primitive characters.

Higher dicot groups (e.g. Salicaceae) may have reticulate tricolpate and tricolporoidate pollen, but unlike the Ranunculales, Trochodendrales, and Hamamelidales they are usually dominated by tricolporate pollen (cf. Fagaceae, Elaeocarpaceae, Flacourtiaceae). In terms of the subclasses of Takhtajan (1966) and Cronquist (1968), it is possible that Albian angiosperms had not evolved beyond the level of the Magnoliidae and lower Hamamelididae, and that the higher Hamamelididae (most of the "Amentiferae"), Dilleniidae, Caryophyllidae, Rosidae, and Asteridae were represented only by ancestors more primitive in pollen morphology and many other characters than their present members. These taxa may have differentiated in the radiation of basically tricolporate groups beginning in the Cenomanian. Some Upper Cenomanian tricolporates already suggest orders of the Rosidae such as the Cornales.

The fossil record indicates that extinct dicot alliances, represented by the Normapolles and *Aquilapollenites*, flourished in the late Cretaceous (cf. Krutzsch, 1963). The possibility of extinct major groups is largely ignored in angiosperm phylogeny, but it is quite relevant, for example, in the "Amentiferae," which may be in large part relics of the group represented by Normapolles pollen.

Since the basic monosulcate pollen type of monocots is common among "ranalean" dicots, the fossil pollen record is ambiguous on the origin of monocots. Though typical *Clavatipollenites* is most like the pollen of some modern dicots, the usually younger reticulate *Liliacidites* type could be either "ranalean" or monocotyledonous. Some Cenomanian pollen is more convincingly monocotyledonous in origin.

The discussion of the last paragraphs shows the consistency of the record with the systems of Takhtajan and Cronquist. In general, "ranalean" theories of angiosperm phylogeny are favored, since the earliest angiosperm pollen is of types characteristic of or restricted to groups considered primitive in such theories. On the other hand, systems which make the wind-pollinated "Amentiferae" primitive become implausible. The Betulaceae, Casuarinaceae, Myricaceae, Rhoipteleaceae, Juglandaceae, and Urticales all have basically triporate pollen (from the Normapolles?), a definitely derived, though ancient, type. The Fagaceae, with generally prolate tricolporate pollen, have a questionable status, but the unusual complex protruding apertures in *Trigonobalanus doichangensis* (Camus) Forman (Erdtman, 1967) suggest a relation to the Normapolles.

CONCLUSIONS

Angiosperm pollen types in the Cretaceous of the Atlantic Coastal Plain appear in essentially the same sequence as in other areas, including the tropics. In the Patuxent and Arundel formations (Barremian?-Lower Albian?) the retipilate monosulcate genus *Clavatipollenites*, apparently the oldest pollen with characters restricted to angiosperms, occurs in a flora dominated by pteridophytes and gymnosperms. Clearly dicotyledonous reticulate tricolpate pollen appears at the base of the Patapsco Formation (Lower-Middle Albian?); tricolpates increase in abundance and diversity in the upper Patapsco (Upper Albian-Lower Cenomanian?), where many show tricolporate tendencies. Definite tricolporates, often psilate and with triangular amb, occur in beds transitional to the Raritan Formation; in the lower Raritan (Upper Cenomanian?) they are joined by the first triporates, *Complexiopollis* and *Atlantopollis* of the extinct (pre-amentiferous?) Normapolles group. In the upper Raritan (Middle-Upper Turonian?), these pass into more advanced Normapolles genera.

The rich flora of the Magothy Formation (Santonian), which includes some forms suggesting modern families, is representative of the Senonian Normapolles province of Europe and eastern North America.

The expansion and diversification of angiosperm pollen in the Cretaceous is believed to reflect the basic adaptive radiation of the group, within which morphological series documenting evolutionary trends and the origin of major types may be recognized. Though the angiosperms may have originated well before the observed radiation, the idea that they were highly differentiated at their first appearance in the fossil record conflicts with the low diversity of Albian angiosperm pollen and the regular sequential appearance of morphological types. Trends such as monosulcate to tricolpate, prolate tricolpate to tricolporoidate to oblate tricolporate to triporate, and retipilate or reticulate to completely tegillate are in good agreement with trends postulated on the basis of comparative morphology and with systems in which the Magnoliidae and lower Hamamelididae are considered primitive and the "Amentiferae" advanced. Considering the evidence for important evolution in pollen characters, it is hoped that the megafossil record of early Cretaceous angiosperms will be re-examined with modern techniques and a more evolutionary-morphological point of view.

TABLE 3. **Evolutionary trends in pollen morphology based on the Cretaceous pollen record**

GENERAL APERTURE TRENDS:
- monosulcate, bilateral symmetry → tricolpate, radial symmetry
- monosulcate or tricolpate → polyporate
- simple colpi → complex apertures

MONOSULCATE GROUP:
- monosulcate → trichotomosulcate, inaperturate, or with several colpoids
- pilate or retipilate → reticulate or completely tegillate

TRIAPERTURATE GROUP:
- tricolpate → tricolporoidate → tricolporate → triporate
- tricolpate → triporate?
- prolate or subspheroidal → oblate, triangular amb, angulaperturate
- retipilate or reticulate → psilate, completely tegillate
- single grains → permanent tetrads
- small size → large size?

NORMAPOLLES GROUP:
- pores nearly simple → pores with atria or vestibula
- no endoplicae → endoplicae
- triangular amb → circular amb

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APPENDIX

LOCALITIES CITED IN TEXT AND FIGURES

PATUXENT FORMATION:

All specimens figured are from the lower Potomac Group exposed in construction of the Susquehanna Aqueduct between Baltimore and Aberdeen, Md., collected by E. T. Cleaves. Locality data are given in Cleaves (1968):

Aq 18 = Cleaves sample no. 18
Aq 27 = " " " 27
Aq 44 = " " " 44
Aq 45 = " " " 45

PATAPSCO FORMATION:

65–1: exposure on E side of parking lot behind Industrial Center on 52nd St., ca. 0.2 mi. N of junction of Kenilworth Ave. (Md. Rt. 201) and Baltimore-Washington Parkway, S of Bladensburg, Md. (Brenner's Station 17). Gray clay bed with cupressaceous twig compressions, 40–50′ above surface of parking lot and Brenner's sample, overlain and underlain by red and gray clay. Subzone B-1 of Zone II, vs. Subzone A of Zone II for Brenner's sample.

65–2a: NW side of West Bros. Brick Co. pit on N side of Sheriff Rd., 1.0 mi. E of Washington, D. C. city limit, ca. 0.7 mi. NW of Highland Park, Md. (Brenner's Station 29). Thin gray clay lens with dicot leaf compressions near top of predominantly red clay, roughly same level as Brenner's collection but toward N side of pit. Subzone B of Zone II.

65–O: exposure on NE corner of Branch Ave. and O St. SE, Washington, D.C. Gray clay lens with lignite bed, grading downward and laterally into red and white clay, and overlain by cross-bedded sands with ironstone concretions ("Raritan" Formation?). Subzone B of Zone II.

65–S: N side of Severn Clay Co. pit, 0.1 mi. N of road connecting Ritchie Highway and Md. Rt. 648, ca. 0.5 mi. SE of Harundale, Md. (Brenner's Station 11). Gray clay lens with dicot leaf compressions just above base of pit, overlain by red clay. Subzone B of Zone II.

B–27: James D. Bethards No. 1 well (Socony-Vacuum Oil Co.), ca. 5 mi. SW of Berlin, Md. (cf. Anderson, 1948). Gray clay core sample from 2735–2751′, provided by Maryland Geological Survey. Subzone B of Zone II.

PATAPSCO-RARITAN TRANSITION ZONE:

68–65: exposure overlooking Chesapeake Bay, ca. 0.6 mi. S of Bodkin Point, Anne Arundel Co., Md. Gray clay exposed just above beach level, passing laterally into red clay, overlain by yellow-white sands with ferruginous ledges. "Raritan" Fm.: Patapsco-Raritan transition zone.

Ch-Bf 127(536–7) and Ch-Bf 127(546–7): well ca. 1.5 mi. NE of Waldorf, Md. (Ch-Bf 127: cf. Hansen, 1968). Medium gray clay core samples from 536–537′ and 546–547′, obtained from Maryland Geological Survey. Near top of "Raritan(?)-Patapsco" Fm.: Patapsco-Raritan transition zone.

TR(1551–3): Toms River Chemical Co. Test Well No. 84, 39° 59′ 3″ N latitude, 74° 14′ 20″ W longitude, Ocean Co., N.J. Gray clay core sample from 1551–1553′, obtained from H. E. Gill through J. P. Owens, U.S. Geological Survey. Near top of Patapsco-Raritan transition zone: samples from 1369–1371′ and 1298–1300′ yield typical Woodbridge pollen and spores.

RARITAN FORMATION:

NJ 2: "Woodbridge, N.J." Light gray clay matrix from specimen of *Magnolia glaucoides* Newberry, N.Y. Botanical Garden Paleobotanical Collections. Woodbridge Clay.

68–8: S side of Sayre & Fisher Brick Co. pit, on S side of Main St., just NE of Sayreville, N.J. Near top of massive dark gray clay exposure. Woodbridge Clay.

68–10: E side of same pit. Medium gray clayey sand at top of massive dark gray Woodbridge Clay.

68–12: NE end of large sand pit ca. 0.5 mi. NNE of Phoenix, N.J. Gray clay capping thick cross-bedded sands. Old Bridge Sand?

68–23: W side of clay pit on N side of Washington Rd., ca. 0.5 mi. E of Parlin, N.J. Near base of thin-bedded gray clay unit, underlain by light gray sand, at low elevations in pit. South Amboy Fire Clay.

68–25: same pit. Near top of same clay unit, exposed just to W and 10–20′ higher. South Amboy Fire Clay.

68–26: same pit. Thin bed of laminated gray clay exposed near top of small hill near NW corner of pit, underlain by white sand, and overlain by thin bed of thinly laminated lignitic sand (68–27). South Amboy Fire Clay or Old Bridge Sand.

68–27: see under 68–26.

68–28: S side of abandoned sand pit off E side of Hillside Ave., just N of high voltage wires, Sayreville, N.J., above and to E of Sayre & Fisher pit (68–8, 68–10). Gray clay lens in predominantly coarse-medium grained sand. Sayreville Sand or South Amboy Fire Clay.

MAGOTHY FORMATION:

68–14: SW corner of Madison Township dump, 0.3 mi. E of U.S. Rt. 9, ca. 0.9 mi. S of junction with Ernston Rd., and 1.5 mi. SSE of Ernston, N.J. Dark gray clay overlain by thin-bedded alternating sands and clays of the Morgan beds of the Magothy Fm., near lowest elevations in dump. Amboy Stoneware Clay (J. P. Owens, pers. comm.).

68–16: bluff overlooking Raritan Bay NE of town of Cliffwood Beach, N.J. Gray silty clay just below contact with glauconitic Merchantville Fm. exposed at top of bluff. Cliffwood beds of Magothy Fm.

Ch-Bf 127(441–2): same well as Ch-Bf 127 samples under Patapsco-Raritan transition zone. Fine gray clayey sand core sample from 441–442′. Near top of Magothy Fm.

Note: Brenner localities are those described in Brenner (1963). Unless otherwise indicated, samples were collected by J. A. Doyle. All slides are located at the Harvard University Paleobotanical Collections.

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